The Effects of Rhizome Severing and Nutrient Addition on Growth and Biomass Allocation in *Diphasiastrum digitatum*

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ABSTRACT.—The effects of severing and fertilization on ramets of *Diphasiastrum digitatum* in an Ohio hardwood forest were examined to determine the extent of young ramet integration. The extent of integration was measured by overall vigor, and by architectural biomass, and growth variables. Vigor decreased with any plant manipulation. Likewise, all measured architectural and biomass variables were smaller in manipulated treatments. Similar negative effects in growth and biomass were seen with severing or fertilization, while a combination of both showed a further decrease in growth variables compared to either of the individual treatments. Severing reduced growth and biomass fifty percent compared to the control, indicating that integration is important in young multi-module ramet development. The results are consistent with other studies suggesting clonal lycopods are highly integrated and emphasizes the importance of integration in young ramets *of D. digitatum* for survival and growth.

Clonal plants are constructed of basic units, called modules, that are iterated throughout the development of a clone and can potentially function as independent members (ramets) of a genetic individual (genet) (Harper, 1977). The existence of connections between ramets or modules of a clone is inherent to its architecture. These underlying vascular connections facilitate the movement and sharing of plant substances (Pitelka and Ashmun, 1985), and thereby permit the clone to function as a physiologically integrated system (Watson and Casper, 1984). As long as connections persist among modules, there is a potential for resource movement (Marshall, 1990; Pitelka and Ashmun, 1985). However, a great deal of variation in the degree of integration within and among clonal plant species has been demonstrated (Jönsdöttir and Watson, 1997). Specifically, clonal plants may vary in their longevity and/or functionality of connections (months to decades), the substances that are moved (minerals, nutrients, carbohydrates, photoassimilates, hormones), and the direction of flow, whether acropetal, basipetal, or bidirectional (see references in Hutchings and Bradbury, 1986; Jönsdöttir and Watson, 1997; Klimeš et al., 1997; Marshall, 1990; Pitelka and Ashmun, 1985).

Such physiological integration can be a major factor influencing survival of clonal plants that retain ramet connections for any period of time (Eriksson and Jerling, 1990; Jönsdöttir and Watson, 1997; Pitelka and Ashmun, 1985). Adaptive advantages incurred by ramets participating in such integration include successful establishment and survival, accelerated maturity, and localized stress recovery (Caraco and Kelly, 1991; Hutchings and Bradbury, 1986; Jönsdöttir and Watson, 1997; Pitelka and Ashmun, 1985). The significance of these adaptive features are seen in cases where disintegration, or fragmenta-

tion, occur. Fragmentation of the genet into smaller ramets or modules may occur naturally through senescence and stress response, or through environmental disturbances such as herbivory, grazing and trampling (Pitelka and Ashmun, 1985). However this fragmentation or disintegration occurs, it has consequences on the growth, biomass and overall survival of the plant in question, most of which remain relatively unexplored in a number of clonal plant species (Charpentier et al., 1998).

Although physiological integration in clonal plants has attracted a great deal of attention in recent years (see references in Marshall and Price, 1997; Jönsdóttir and Watson, 1997; Pitelka and Ashmun, 1985), most studies have focused on angiosperms rather than lower plants such as pteridophytes. Examining the clonal patterns and processes of integration in pteridophytes offers not only a complete view of the plant kingdom, but also offers an evolutionary view of integration in lineages of clonal plants that have existed in many habitats and geologic time periods (Dyer, 1979). In particular, few studies have investigated the extent of physiological integration in lower plants such as lycopods (Callaghan, 1980; Carlsson et al., 1990; Headley et al., 1985; 1988a; 1988b) and those that do concern lycopods involve relatively few, common species that do not reside in North America. *Diphasiastrum digitatum* (Dillenius ex. A. Braun) Holub is a North American member of the Lycopodiaceae that is relatively common in its native habitat but has been little studied in light of its clonality and physiological integration (Jönsdóttir and Watson, 1997; Lau and Young, 1988). Previous examination of this species' physiological integration has focused on the survival of older modules (Lau and Young, 1988), whereas generalized studies of clonal plants indicate that younger ramets of clonal plants are usually most dependent on connections to the parent ramet (Hutchings and Bradbury, 1986).

In this study, we examine the effects of severing and nutrient addition on newly developing ramet growth in *Diphasiastrum digitatum* in order to determine the general extent of its physiological integration and to determine how it directly responds to disintegration from the parent clone and to a localized increase in nutrients. We hypothesize that during early development, artificially severing rhizome connections to the parent will significantly decrease the vigor, growth, and biomass of young ramets. Furthermore, we hypothesize that adding nutrients to the sterile edaphic environment characteristic of *D. digitatum* will increase the vigor, growth, and biomass of younger ramets.

METHODS AND MATERIALS

STUDY ORGANISM.—*Diphasiastrum digitatum* is a common understory herb in the northeastern United States (Wagner and Beitel, 1996) that forms dense clonal patches through vegetative growth. This evergreen perennial displays a rhizomatous growth form, whereby horizontal creeping stems bear distinctive fan-like, dimorphic (vegetative and reproductive) vertical shoots and adventitious roots. *Diphasiastrum digitatum* is the most common species of its genus in North America (Wagner and Beitel, 1996), and is found in a number of

habitats, including hardwood and conifer forests as well as open shrubby areas (Cody and Britton, 1989; Wagner and Beitel, 1996). Many members of this and other closely related genera in the temperate region are characterized as weedy and are believed to grow in relatively infertile soil conditions (Page, 1979; Tryon and Tryon, 1982).

The life span of most vertical shoots is approximately four to six years (Primack, 1973; Railing and McCarthy, unpublished data). Rhizome connections may persist for some time before decaying and thereby separating previously connected ramets. This type of vegetative reproduction has been noted as more common than sexual reproduction (Primack, 1973) in *Diphasiastrum digitatum,* most likely reasoned so because of the unsuccessful or poor spore germination witnessed in gametophyte cultures, rather than in nature (Roberts and Herty, 1934; Whittier, 1981; 1998).

STUDY AREA.—Strouds Run State Park (SRSP) is located in Athens County, Ohio at 39°20′N (latitude) and 82°5′W (longitude), in the southeastern foothills of the state. In the early twentieth century, the area was disturbed by grazing and timbering activities. As such, most of the forests are considered to be even-aged second-growth. What is now known as SRSP was acquired for conservation purposes in the late 1940's and early 1950's by the State of Ohio and eventually became a state park in 1959. The park spans over 1100 ha on Appalachian Ohio's unglaciated Allegheny plateau, and is centered around a man made watershed, Dow Lake. The topography consists of a number of steep hills and ravines believed to be remnants of glacial meltways. Soils in this region of Ohio are classified as Inceptisols (Brady, 1984) and soil conditions throughout the park are characterized as being moderately deep to deep, well-drained, and mostly loamy (typic hapludalfs), originating from sandstone, siltstone, shale, and limestone parent material (National Cooperative Soil Survey, 1985). Precipitation is relatively evenly distributed throughout the year and ranges from 5–10 cm per month, with July being the wettest month and October the driest. Mean temperatures (high/low) are 29/18 C for July and 2/−8 C for January (Midwestern Climate Center, 1999).

The vegetation of SRSP is primarily deciduous forest cover and can be classified as mixed mesophytic (*Acer* spp., *Aesculus octandra, Fagus grandifolia,* and *Liriodendron tulipifera*) in the lowlands and mixed oak or oak-hickory in the uplands (*Quercus alba, Q. rubra, Q. velutina* and *Carya glabra, C. ovata*). A number of white pine plantations (*Pinus strobus*) are also present in the park (<10% of vegetation), having been planted by conservation corps for watershed protection. There are also sporadic old-fields, grassy meadows, and maintained turf grass habitats. The herbaceous layer of the woodlands is largely dependent upon the overstory vegetation and there is considerable diversity of both microhabitats and species (Payne, 1957; Greer et al., 1997).

FIELD METHODS.—Ten *Diphasiastrum digitatum* patches were located within SRSP. In June 1998, 4 apical rhizome tips, approximately 1–2 m apart, were haphazardly located around the perimeter of each patch. Rectangular quadrats (0.25 × 2 m) were established around each of the four rhizome tips such that

the rhizome was situated 0.5 m into the quadrat along the longest dimension. Quadrats within each patch were randomly assigned to one of four treatment groups. The first treatment group (C) served as the control, and remained un-manipulated throughout the duration of the experiment. Rhizomes in the second treatment group (S) were severed at their entrance into the rectangular quadrat. Quadrats assigned to the third treatment group (F) were treated with a standard 10-10-10 inorganic fertilizer (Dragon All Purpose Plant Food) at a prescribed monthly rate (ca. 100 g fertilizer per m^2) for perennials. Rhizomes in the fourth treatment group (SF) were subject to both severing and fertilization treatments. Other above ground vegetation within quadrats was clipped and treatments were applied after quadrat establishment in June 1998.

In August 1998 vigor observations were made in situ before excavating all rhizomes. Rhizomes were assigned to one of three vigor categories that were based on health and color. High vigor (HI) indicated a rhizome or ramet with high health and a green to bright green color, similar to the rest of its original patch. Moderate vigor (MD) and low vigor (LO) referred to a ramet that displayed moderate health and green to yellow color and poor health with yellow to brown color, respectively. Excavated ramets were subsequently measured, oven dried at 80 °C for ca. 48 hours and weighed. Data were collected to reflect growth and biomass patterns since the initial treatment application. Variables examined upon ramet collection include total growth length (cm), number of new shoots and roots initiated, mean internode and shoot length (cm), and aboveground (internode and shoot) biomass (g) for each ramet.

ANALYTICAL METHODS.—A G-test (Chi-Square Goodness-of-Fit Test) was used to analyze the homogeneity of vigor categories among treatment groups (Sokal and Rohlf, 1995) with the null hypothesis that there are no differences in ramet frequency among the twelve possible classes (i.e., treatment/vigor combinations). In order for G to better approximate the chi-square statistic, the Williams correction factor was applied as recommended by Sokal and Rohlf (1995).

A Multivariate Analysis of Variance (MANOVA) was used to test for overall significant treatment effects across all growth and biomass parameters measured using the Wilk's Lambda test statistic (Hintze, 1997). A randomized complete block design MANOVA was employed using treatment group as a fixed effect and patch as a random effect. Data sets were checked for normality, equal variance, and equality of covariance using the D'Agostino Omnibus test (D'Agostino et al., 1990), Modified-Levene Equal-Variance test, and Box's M test, respectively, to meet the assumptions of MANOVA. Those failing the normality assumption were corrected using either log_{10} or square-root transformations.

Planned (a priori) comparisons (Dowdy and Wearden, 1991) were used to test for significant differences among treatment groups according to the three hypotheses. We used the first hypothesis (H_1) to test for significant differences between the control and all other treatments (C vs. S,F,SF), the second (H_2) to test for differences between treatment types (S vs. F) and the third (H_3) to test

TABLE 1. Observed frequency of ramets within each treatment group according to vigor category, including G-test (Chi-Square Goodness-of-Fit) results. Note that when the cell element marked with an asterisk is removed, G = 14.8 and P > 0.1.

Treatment Group	Vigor Category		
	HI	MD	LO
Control (C)	9*	1	0
Sever (S)	5	5	0
Fertilize (F)	3	6	1
Sever and Fertilize (SF)	0	4	6
G = 24.9, P < 0.01			

for an additive effect of treatment types (SF vs. S,F). The above planned comparisons were only used on those variables significantly contributing to treatment effect within the MANOVA. All statistical analyses mentioned above were conducted using NCSS statistical software (Hintze, 1997) with an alpha of 0.05 used to test hypotheses.

RESULTS

The results of the G-test used for the vigor study indicated that significant differences (P < 0.01) among vigor-treatment combinations existed (Table 1), thereby rejecting the overall null hypothesis and indicating that *Diphasiastrum digitatum* ramets within vigor categories did reflect a treatment effect. However, upon closer examination, one class (Treatment C—HI vigor) may be driving the significance in this analysis (Table 1). In an exploratory procedure, the aforementioned class was removed from the analysis to test for significant differences among the remaining other classes. The resultant G-Test indicated that the classes were then homogeneous (Table 1). Hence, the control group displayed the highest vigor, and any perturbation (treatments S, F, SF) of the ramets affected their health and coloring, reducing vigor to either the moderate (MD) or poor (LO) categories.

Although there are no significant (P = 0.347) differences among patches for the measured variables (Table 2), there are significant differences among treatment groups (P = 0.044). Individual one-way ANOVAs for each of the growth and biomass variables in the MANOVA analysis indicate that shoot biomass, total growth, new shoots initiated and new roots initiated are the specific variables measured that reflect significant differences among treatment groups with high power (Table 3). In addition, relatively little to no significant differences in mean internode and shoot height among treatment groups were witnessed (Table 3). However, confidence in this finding is low due to the minimal statistical power in the respective F-tests. In order to meet the multicollinearity assumption of MANOVA, both above ground biomass and internode biomass variables were dropped from the analysis and examined seperately using one-way ANOVAs. Above ground biomass (P = 0.004) and internode biomass (P = 0.002) did differ significantly among treatment groups (Table 3).

TABLE 2. Multivariate Analysis of Variance (MANOVA) test for differences among treatments and patches across all variables measured. Above-ground biomass and internode biomass variables were removed to meet multicollinearity assumption.

Source	Wilk's Lambda	df1	df2	F-ratio	P-value
Treatment	0.306	18	63	1.81	0.044
Patch	0.125	54	117	1.09	0.347

Overall, the plants in any manipulated group (S, F, or SF) displayed a 50% or more decrease in growth and biomass (Fig. 1). The first planned comparison (H_1: C vs. S,F,SF) was significant across all variables examined ($P < 0.01$) with any manipulation of the rhizomes leading to a decrease in the measured variables (Fig. 1). There was no significant difference between treatment types for all variables as indicated by the second planned comparison (H_2: S vs. F). Results of the third planned comparison (H_3: SF vs. S,F) indicate that only the new shoots initiated ($P = 0.03$) and new roots initiated ($P = 0.08$) showed an additive treatment type effect.

DISCUSSION

The fact that severing showed a decrease in growth and biomass compared to the control group supports our hypothesis that *D. digitatum* ramets should show dependency upon parental connections and are therefore highly integrated at the studied hierarchical level of clone structure. A number of other studies on clonal angiosperms have revealed similar decreases in growth and biomass in severed versus non-severed ramets (Ashmun et al., 1982; Charpentier et al., 1998; Hartnett and Bazazz, 1983; Jönsdóttir and Watson, 1997). However, the severity of such disintegration often depends upon the size and age of the ramet severed from the parent clone—the youngest and smallest ramet segments severed often suffer the most damage to vigor (Hartnett and Bazzaz, 1983; Jönsdóttir and Watson, 1997; Pitelka and Ashmun, 1985). However, when comparing the current study using younger, interconnected ramets to those based on older, independent ramets of *D. digitatum* (Lau and Young, 1988) the effects of severing are essentially the same. This suggests that the increased hardship likely incurred by younger ramets is not seen when those ramets are part of interconnected multi-module units.

Jönsdóttir and Watson (1997) classify *Diphasiastrum digitatum* as displaying full integration in large clonal fragments, and in turn place other pteridophytes and angiosperms within this category. Bracken (*Pteridium aquilinum* (L.) Kuhn) is a widely studied economic pest that displays a number of growth characteristics similar to those of *D. digitatum*, although the former is much more aggressive and has a different growth habit. Both are clonal pteridophytes that grow by means of a perennating, indeterminate rhizome bearing fronds or shoots, sometimes occupying large patches of the landscape (Parks and Werth, 1993). Experiments originally aimed at finding a method of controlling bracken

TABLE 3. Results of one-way ANOVA tests for variables significantly contributing to treatment effect in previous MANOVA. Asterisks denote one-way ANOVAs for two variables originally omitted from MANOVA.

Variable Measured	df	MS	F-ratio	P	Power
Above-Ground Biomass (g)*	3	0.28	5.71	0.004	0.82
Internode Biomass (g)*	3	0.57	6.33	0.002	0.86
Shoot Biomass (g)	3	1.69	6.92	0.001	0.89
Total Growth (cm)	3	0.37	4.69	0.009	0.73
Mean Internode Length (cm)	3	0.51	0.10	0.959	0.06
Mean Shoot Height (cm)	3	0.50	2.69	0.066	0.47
Number New Shoots	3	9.90	8.36	0.001	0.95
Number New Roots	3	0.34	5.67	0.004	0.82

have revealed that severing bracken rhizomes does not elicit the same severe effect on plant growth and biomass witnessed in the present and other studies concerning *D. digitatum* (Lau and Young, 1988). In fact, seasonally-timed, repetitive cutting of above and below ground rhizomes, as well as above ground fronds of bracken is needed to significantly affect respiration and assimilate translocation and ultimately reducing the plant's spread within an area (Lowday, 1986; Lowday et al., 1983). This reaffirms the findings that *D. digitatum* is extensively integrated, particularly in comparison to another clonal pteridophyte.

Comparisons between the physiological integration of the mayapple (*Podophyllum peltatum*, L.) and *D. digitatum* are also useful as these two herbs often occupy similar habitats in the eastern deciduous forest and are frequently found growing near each other. Although the *P. peltatum* tends to have a greater degree of lateral spread than *D. digitatum*, both are extensive integrators (Jönsdöttir and Watson, 1997) that reproduce mainly through vegetative processes, and thereby are severely affected by severing treatments that interfere with acropetal transport to younger ramet fragments in particular. However, the severity of severing in mayapple depends upon the size of that ramet fragment severed (Jönsdöttir and Watson, 1997), unlike the current and other studies (Lau and Young, 1988) concerning *D.digitatum* ramets, which display the same reduction in growth and biomass, regardless of ramet size or age. This comparison suggests that *Diphasiastrum digitatum* is dependent upon integration at any scale within a ramet, indicating that integration is an adaptive trait, possibly because of the resource-poor environments it inhabits (Jönsdöttir and Watson, 1997).

Diphasiastrum digitatum ramets in the fertilized treatment group (F) showed declines in biomass and growth patterns (Figure 1) equivalent to the severed treatment group (S) compared to the control group (C). This result does not support our original hypothesis that fertilization will increase the growth and biomass of *Diphasiastrum digitatum*. Upon closer examination of the experimental methods, the nitrogen source within the fertilizer may be a possible explanation. The fertilizer used within the current experiment delivered nitrogen in two forms: ammonium nitrogen (3.91%) and urea nitrogen (6.09%).
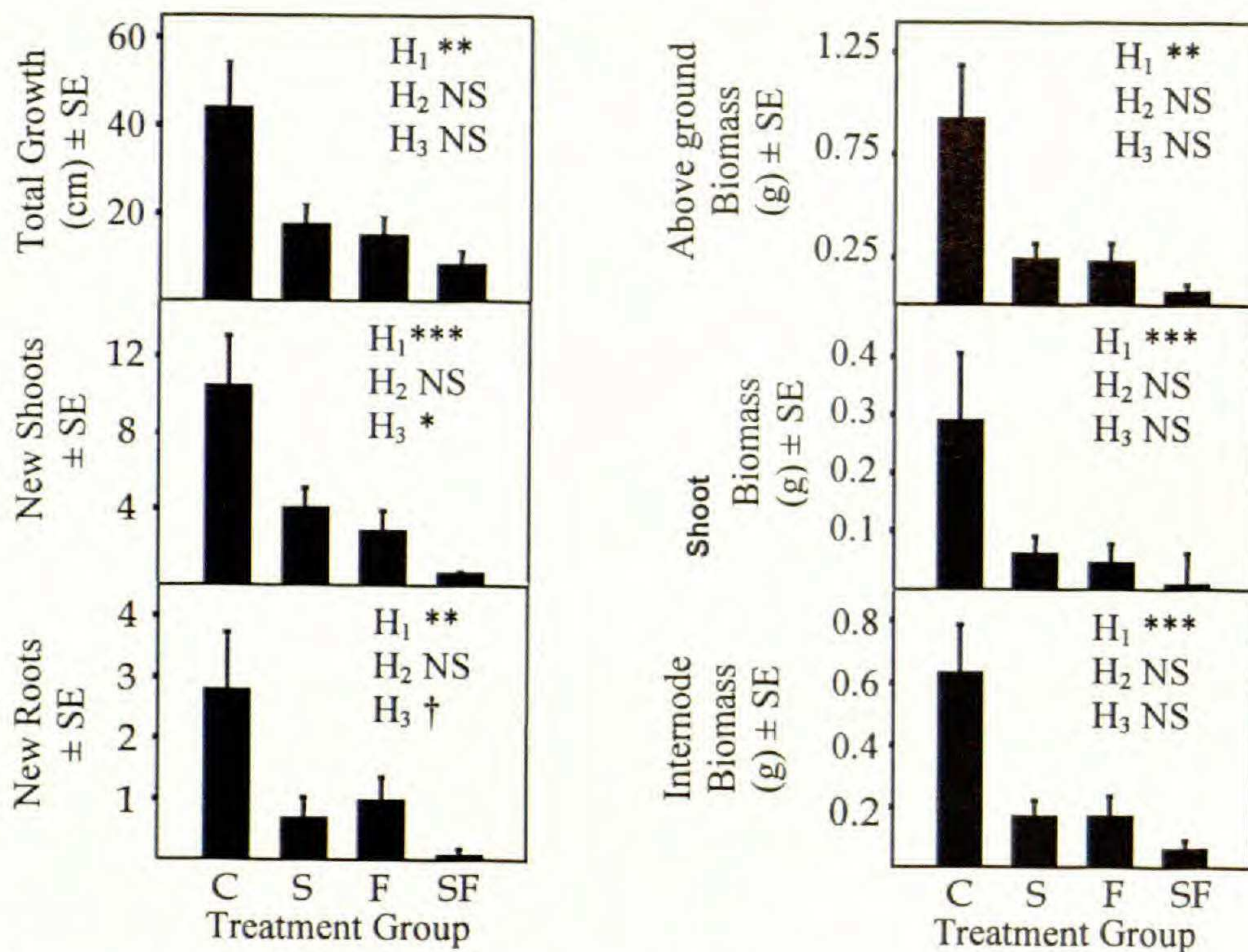
FIG. 1. Mean values (± 1 standard error) of growth and biomass variables under each of four treatment conditions (A = control, B = severed, C = fertilized, D = severed and fertilized). Significance levels for each of the three planned comparisons, (H_1, H_2, H_3), are denoted as such: *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, † = $P < 0.1$.

A number of studies suggest that nitrate is the ideal deliverable form of nitrogen in fertilizers, whereas ammonium and urea forms can negatively affect health of some plants, particularly in combination with lower edaphic pH (Feng and Barker, 1992; Magalhäes and Huber, 1989). Such investigations of nitrogen form on crop plant performance have supported that ammonium and urea nutrition stimulate further acidification of the immediate environment, and the foliar production of ethylene and accumulation of ammonium in shoots (Feng and Barker, 1992). The proximate effect of ammonium toxicity witnessed on crop plants includes a decrease in both growth and biomass accompanied by plant wilting, chlorosis, and necrosis of above-ground parts (Cao and Tibbitts, 1998; Kpodar et al., 1992). Similar symptoms of ammonium toxicity were observed in this study for the two treatment groups receiving fertilizer (F and SF).

For the most part, studies concerning physiological integration in lycopod species have focused strictly on documenting water and/or nutrient movement and storage throughout the organism (Callaghan, 1980; Headley et al., 1985; 1988a; 1988b). Consequently, further study is needed to determine the type(s) of ramet transport (water, nutrients, carbohydrates) that is the most crucial to lycopod or clonal plant survival in addition to determining short and long-term plant architectural and physiological responses to a dis-integration event affecting the crucial transport. Such examinations would lend greatly to the

understanding of the presence of clonal plants throughout evolutionary and ecological history.

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